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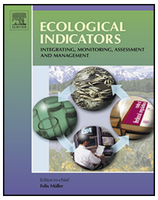

An indicator highlights seasonal variation in the response of Lepidoptera communities to warming

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ABSTRACT

The impacts of climate change on species and ecosystems are increasingly evident. While these tend to be clearest with respect to changes in phenology and distribution ranges, there are also important consequences for population sizes and community structure. There is an urgent need to develop ecological indicators that can be used to detect climate-driven changes in ecological communities, and identify how those impacts may vary spatially. Here we describe the development of a new community-based seasonal climate change indicator that uses national population and weather indices. We test this indicator using Lepidopteran and co-located weather data collected across a range of UK Environmental Change Network (ECN) sites. We compare our butterfly indicator with estimates derived from an alternative, previously published metric, the Community Temperature Index (CTI).

First, we quantified the effect of temperature on population growth rates of moths and butterflies (Species Temperature Response, STR) by modelling annual variation in national population indices as a function of nationally averaged seasonal variation in temperature, using species and weather data independent of the ECN data. Then, we calculated average STRs for annually summarised species data from each ECN site, weighted by species' abundance, to produce the Community Temperature Response (CTR). Finally, we tested the extent to which CTR correlated with spatial variation in temperature between sites and the extent to which temporal variation in CTR tracked both annual and seasonal warming trends.

Mean site CTR was positively correlated with mean site temperature for moths but not butterflies. However, spatial variation in moth communities was well explained by mean site summer temperature and butterfly communities by winter temperature, respectively accounting for 74% and 63% of variation. Temporal variation in moth and butterfly CTR within sites did not vary with the mean annual temperature but responded to variation in the mean temperature of specific seasons. There were positive correlations between moth seasonal CTRs and seasonal temperatures in winter, spring and summer; and butterfly seasonal CTRs and seasonal temperatures in winter and summer. Butterfly CTR and CTI both correlated spatially and temporally with winter temperature.

Our results highlight the need for seasonality to be considered when examining the impact of climate change on communities. Seasonal CTRs may be used to track the impact of changing temperatures on biodiversity and help identify potential mechanisms by which climate change is affecting communities. In the case of Lepidoptera, our results suggest that future warming may reassemble Lepidoptera communities.

1. Introduction

The impacts of climate change on species and ecosystems are increasingly evident (Parmesan and Yohe, 2003; Pearce-Higgins and Green, 2014). Polewards and uphill range expansions have been seen across many taxa, accompanied by range retractions at warm edges (Franco et al., 2006; Hickling et al., 2006; Chen et al., 2011). Community changes have been widely observed: generalist species are increasing in abundance relative to specialists (Warren et al., 2001; Davey et al., 2012; Le Viol et al., 2012), whilst warm-associated species have tended to increase relative to those that occupy cooler climates (Devictor et al., 2008, 2012; Jiguet et al.,

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2010). To minimise biodiversity loss, there is a considerable need to identify the species most likely to be vulnerable to climatic changes (Pacifici et al., 2015). These are likely to include: species with less opportunity or ability to adapt through phenological plasticity (Vedder et al., 2013), habitat specialists (Davey et al., 2013), species sensitive to climatic impacts on other species with which it interacts strongly (Ockendon et al., 2014), and species with a dispersal barrier polewards of their range extent (Foden et al., 2013). There is also a need to predict where climate change will cause the greatest ecosystem disruption.

Tracking the impacts of climate change on species and ecological communities is complex and challenging, as it potentially involves effects of multiple climatic, and other, drivers operating through a range of mechanisms. Despite this, a number of summary indicators have been developed that appear to separate species by their likely response to warming or climate change, and that can be used to track the potential impacts of climate change on ecological communities (Thuiller et al., 2005; Devictor et al., 2008; Gregory et al., 2009). For example, the Species Temperature Index (STI) describes the mean temperature across a species' range, and is used to derive the Community Temperature Index (CTI), which is the mean STI across species present at a site, weighted by their abundance. Changes in CTI through time have been shown to indicate long-term community responses to warming in both birds and butterflies (Devictor et al., 2008, 2012). Alternatively, individual climate envelope models have been used to separate species by their likely response to climate change. The divergence in population trends between species projected to increase in response to climate change and those projected to decline then provides another potential climate change indicator (Gregory et al., 2009). In these studies, and here, a community is defined as the collection of individuals present at a site within a taxonomic group. Both methods use spatial information about species' distributions to describe the association of that species with climate, and therefore they are limited to taxonomic groups with well-understood spatial distributions such as birds, butterflies and plants. Furthermore, climatic niche models have a number of problems which may limit their ability to predict and indicate climate change impacts (Pearson and Dawson, 2003; Hampe, 2004). In particular, models based on a climatic envelope take little account of interactions between species or their ability to shift range (Pearson and Dawson, 2003).

Here we trial an alternative method that characterises species' responses to temperature by modelling temporal variation in annual abundance as a function of temperature (the Species Temperature Response; STR), rather than using spatial distribution. This allows metrics of community change to be derived from the average STR at a site in a year, weighted by relative abundance (the Community Temperature Response; CTR), in a manner similar to Devictor et al. (2008). Further, this method may also be adapted to summarise responses across different seasons and thereby provide an indication of the times of year when species respond most to climate change impacts, which may be helpful in identifying the potential mechanism underpinning observed community changes. If successful, this method may be used where there is long-term temporal monitoring at any spatial scale (results could be obtained using only a single site), but relatively little information on species' range extents. UK examples of taxa which meet these criteria include moths, aphids and bats, and this indicator may therefore be widely applicable.

In this paper, we used national monitoring data to calculate STR for a range of moth and butterfly species. We then tracked changes in the communities of both groups across a network of sites with biological and environmental recording that included meteorological data (Environmental Change Network sites; ECN). We assessed the ability of the CTR metric to predict both spatial and temporal variation in annual and seasonal temperatures. Agreement between the CTR metric and temporal temperature variation would indicate rapid responses to climate change, for example, caused by direct effects on demographic rates or species' interactions. Agreement between the CTR metric and spatial temperature variation would indicate that temperature is an important determinant of species' current spatial distribution and would thus provide an indication of the sensitivity of communities to long-term climate change. To be effective, an indicator must be able to measure rapid responses to temporal temperature variation, and provide evidence that these will lead to long-term community changes as indicated by spatial patterns in CTR. We compared the sensitivity of moth and butterfly communities to warming by comparing the strength of relationship between the moth and butterfly CTR indicators and spatial and temporal temperature variation. Finally, we also compared the ability of butterfly CTR to spatially and temporally track temperature with that of the already published butterfly CTI (Devictor et al., 2012).

2. Material and methods

2.1. National data

We used national population indices to characterise the extent to which a species' population was positively or negatively correlated with temperatures (species' temperature response, STR). Data required to calculate the STRs were taken from two national monitoring schemes, one for butterflies and one for moths. Butterfly data were obtained from the UK Butterfly Monitoring Scheme (UKBMS). We only used butterfly data from sites in England because of a bias towards England in the early years of the survey compared with the current distribution of sites, which are more widespread. This restriction reduced the chance of temporal and spatial bias affecting the national trends. There are over 1000 English sites monitored in the UKBMS. The moth data were derived from thirteen long-running sites monitored by the Rothamsted Insect Survey (RIS). Most of these sites are in England and Wales (see Supplementary Information (SI) Fig. 1 for a map of the RIS moth traps). We only used data from the thirteen sites that were consistently monitored from 1978, hence avoiding the need to consider temporal biases in the data.

Using these data, we calculated population indices for butterflies from 1976 to 2011, and for moths from 1975 to 2010 using TRIM (Pannekoek and van Strien, 1998). Annual counts at sites were modelled as a function of both categorical site and year effects using a Poisson General Linear Model (GLM) with a standard log link accounting for serial correlation and overdispersion (Ter Braak et al., 1994; Freeman and Newson, 2008). Only species with at least one record per year were included, allowing us to calculate STR values for 46 butterfly and 265 moth species (see SI Table 1).

We related the national population indices to nationally averaged weather data (see Section 2.2). For this we used data from Met Office UK Climate Projections 2009 (UKCP09) gridded monthly datasets averaged across England (for butterflies) and the UK (for moths) (Perry and Hollis, 2005).

2.2. Species temperature response

We used a simple model to characterise each species' temperature response (STR), i.e. the extent to which their populations were positively or negatively correlated with mean seasonal temperatures throughout a year. Annual population growth was calculated from the national population indices ($y_t = \ln\ (n_t/n_{t-1})$, where n_t is the annual national population index in year t). Population growth was modelled against annual variation in seasonal temperatures (throughout, we define seasons as follows: Winter, Dec–Feb;

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